Conserving Evolutionary Process in the Sky Islands of Northern Mexico

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The mixed pine-oak woodlands of the Sierra Madre mountain chains in Mexico are a significant focus of biodiversity for North America. Harboring about a third of the world's pine and oak species, this high-elevation region is a major center of endemism for birds, reptiles, and amphibians, including several endemic bird genera such as the thick-billed (*Rhynchopsitta pachyrhncha*) and maroon-fronted (*R. terrisi*) parrot and the Sierra Madre sparrow (*Xenospiza baileyi*). This area was recently selected by Conservation International as an important "hotspot" – a distinction it shares with the world's other most "biologically rich and endangered ecoregions." This double-edged distinction is exemplified by the imperial woodpecker (*Campephilus imperialis*), the world's largest woodpecker, endemic to Madrean highlands and now likely extinct.

A view of the Sierra del Carmen, a sky island in Coahuila, Mexico. Chihuahuan desert in the lowlands gives way to conifer forest at high elevations. Sky islands in Texas can be seen in the distance.

As the Sierra Madres approach the United States border, their massive, interconnected cordillera give way to a series of broken mountain ranges that are isolated from one another by lowland desert. These "sky islands" rise serenely from the desert and provide a refuge for cool-adapted species and a migratory destination for birds and the humans who seek them out. Biologists have long been fascinated by sky islands for the same reason that oceanic islands have held their fancy since Darwin's time: they provide a natural laboratory of replicated habitats for the study of evolution. Moreover, each sky island contains altitudinal zonation of habitats, meaning that habitats are stacked one on top of another, beginning at low elevations with desert and culminating with alpine conifer forest. As a result, ecological transitions that would take thousands of kilometers to traverse driving north by car take place over just a few kilometers in sky islands.

Plant and animal populations that span these ecological transitions experience drastically different environments, both abiotic (e.g., rainfall and temperature) and biotic (e.g., food resources, competitors, and predators). In the terms of evolutionary biology, these differences result in divergent natural selection acting between different ends of the habitat gradient, which, if strong enough, can generate observable differences between populations that are connected by genetic exchange (i.e., gene flow) and, therefore, are likely to remain similar in the absence of a strong diverging force. This process is called "divergence with gene flow." At one time it was considered impossible – or at least rare enough to be dismissed as

evolutionarily unimportant – but it is now being documented widely in nature with important implications, not just for evolution, but also for conservation.

As part of my dissertation, I have been investigating divergence with gene flow along a particularly dramatic elevation and habitat gradient in the Sierra del Carmen of northern Coahuila, Mexico (Fig. 1). This mountain range, lying just 40 km south of Big Bend National Park in Texas, is exceptional because its distance from colonizing sources has prevented populations of many bird species from becoming established there. This has allowed several species already present in the Sierra del Carmen to be able to expand their ecological niches to include habitat in which they are normally absent. This has set the stage for divergent natural selection to act on these populations and potentially generate differences between high and low elevations.

No species in the Sierra del Carmen has expanded its niche more conspicuously than the Mexican jay (*Aphelocoma ultramarina*). Throughout most of its geographic range, the Mexican jay is found in a narrow belt of mid-elevation mixed pine-oak-juniper woodland between 1,350 m (4,400 ft) and 1,800 m (5,900 ft), and is replaced at lower elevations by the western scrub-jay (*A. californica*) and at higher elevations by the Steller's jay (*Cyanocitta stelleri*). In the Sierra del Carmen, Mexican jays have expanded their altitudinal range in the absence of these species and now occupy a gradient that spans from oak scrub in low-elevation canyons at 1,200 m (4,000 ft) to moist conifer forest on the highest peaks at 2,700 m (8,900 ft).

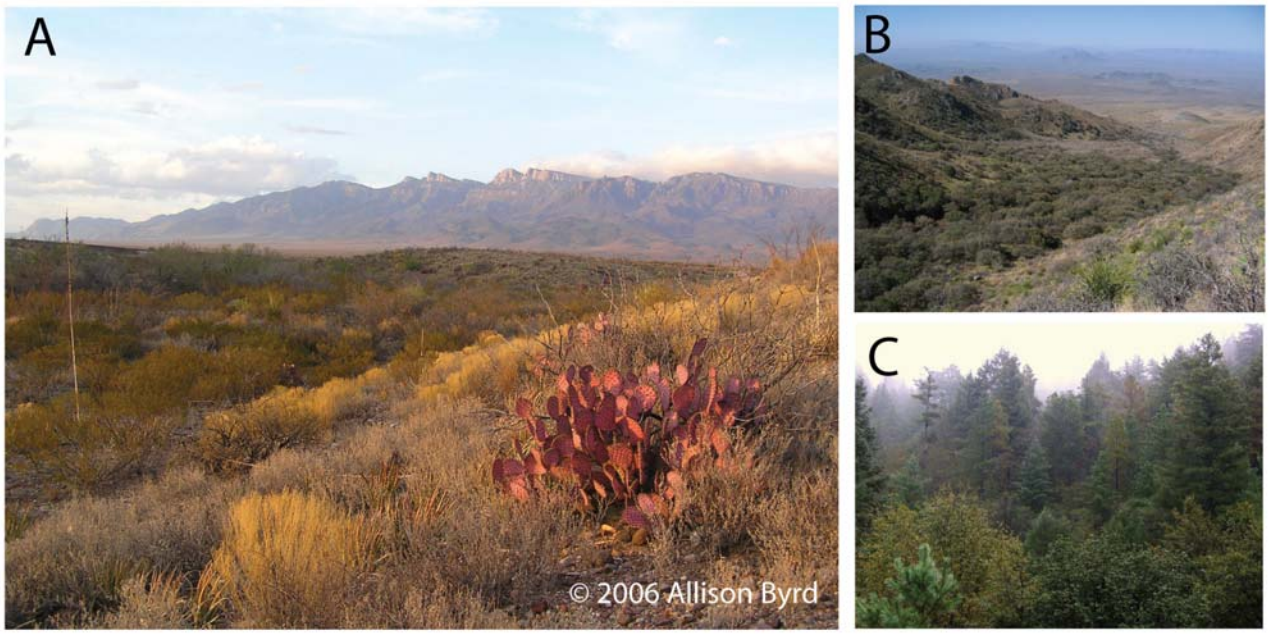

Figure 1. (A) The Sierra del Carmen, a sky island in northern Coahuila, Mexico, rises to nearly 2,700 m (8,900 ft) from the Chihuahuan desert. (B) Low elevation woodland at 1,500 m (5,000 ft) composed mainly of oaks (*Quercus*). (C) High elevation conifer forest at 2,400 m (7,900 ft) composed mostly of pines (*Pinus*).

My study sought to determine if jays at high elevations had become adapted to feeding on pine seeds whereas jays at low elevations had adapted to acorns. Mexican jays do not migrate and rarely disperse far from their natal flocks, so they are highly dependent for winter survival on local seed crops. Nevertheless, diversification in beak shape would be truly remarkable considering that these populations are only 3 to 15 km apart with no obvious barriers to dispersal between them. We mist-netted jays at high and low elevations, measured them in various traits, took blood samples to assess gene flow, and released them at their point of capture. Because we had reason to suspect from previous studies that the hook at the end of the beak might play a large role in feeding adaptation, we took photos of every jay and measured hook length digitally.

Results indicate that divergence with gene flow has produced different beak types – straight beaks at high elevations that act like tweezers to extract pine seeds from cones and hooked beaks at low elevations

that are maladaptive for this purpose but might be useful for husking acorns (Fig. 2). These results are particularly interesting because they shed light on niche expansion – the invasion of novel habitats – which has been a precursor to some of the most spectacular animal radiations (such as the Galapagos finches, Caribbean *Anolis* lizards, and African cichlid fish). The exact sequence of events leading from niche expansion through the type of differentiation we have documented in the beaks of Mexican jays to eventual reproductive isolation and speciation is not well understood. My study suggests that the initial steps in this process can involve divergence with gene flow along ecological gradients.

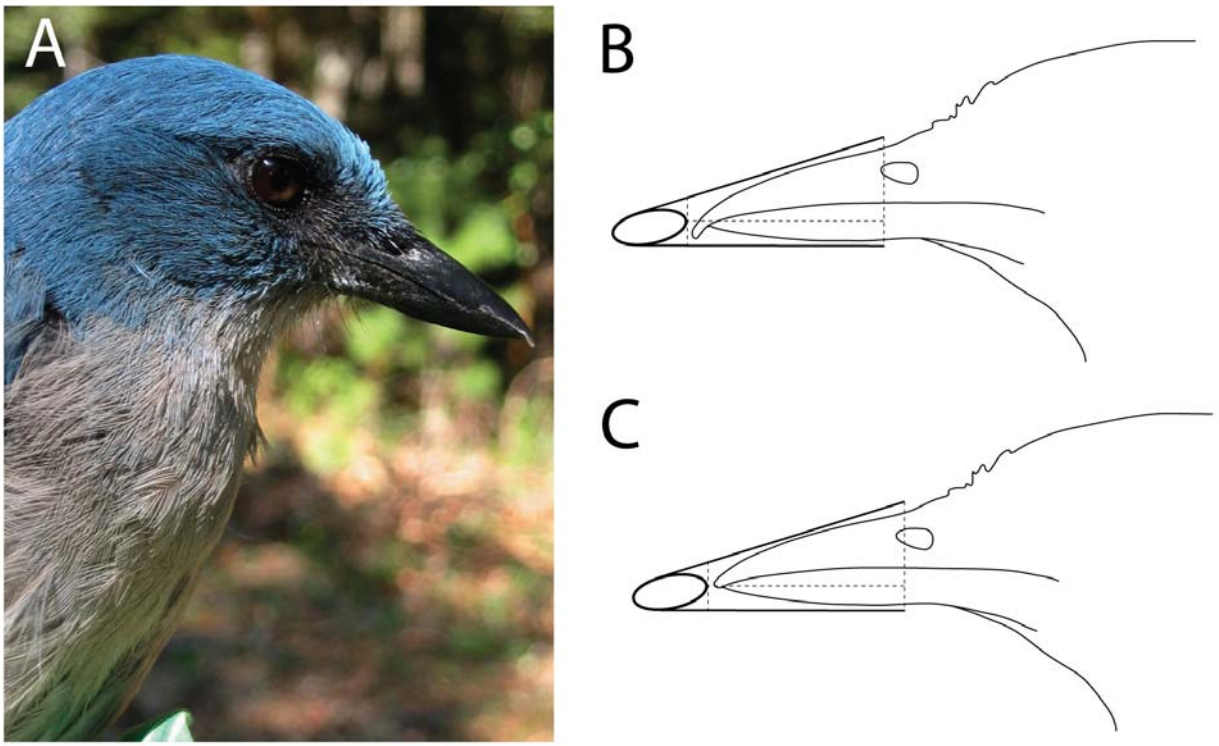

Figure 2. (A) Mexican jay. Beak differences between jays at low (B) and high elevations (C) in the Sierra del Carmen. Jays at high elevations have, on average, smaller hooks, which are not well adapted to extracting seeds from pine cones. Note that small differences in hook size (of 1 mm or less) can lead to large differences in functionality.

The Sierra del Carmen and the surrounding area are gaining attention as a premier conservation area collectively known as the El Carmen-Big Bend Transboundary Megacorridor. A private company, CEMEX, working in conjunction with local, national, and international non-governmental organizations (NGOs), has dedicated itself to preserving this region and its wilderness for long-term ecological sustainability. At the same time, the preservation of evolutionary process – such as natural selection along ecological gradients – is gaining currency as a method for ensuring species survival in a dynamic and changing world. Insights from my research will hopefully aid in the incorporation of evolutionary process into the nascent conservation agenda for this region where its role in generating diversity is so evident.

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